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BASELEVELING AND ITS FAUNAL SIGNIFICANCE, WITH ILLUSTRATIONS FROM SOUTHEASTERN UNITED STATES.

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In considering some of the peculiarities of the fauna of the southeastern United States I wish to call attention to certain principles that are fundamental to an understanding of the present distribution of many forms of life, especially those of land and fresh-water. Especial stress is laid on the relation of physiographic changes, and baseleveling in particular, to faunal changes and to the differentiation of land and fresh-water animals.[1]

The necessity of correlating the results of baseleveling, and river histories in particular, with the distribution of habitats and their fauna, was very emphatically impressed upon me in connection with some studies upon the Pleuroceridæ of southeastern United States. This relation was clearly demonstrated to me when I learned that the former course of the Tennessee River from Chattanooga was direct to the Gulf *via* the Coosa-Alabama system. Having thus become fully convinced of the great biological significance of the baseleveling factors, it was of considerable interest that I later learned that Woodworth (**'94**) had already appreciated this significance.

In a general way, this relation of physiography to topographic and geographic distribution has been well understood, but such studies need to be carried out in more detail. The geologists, from their familiarity with the physiographic processes, seem to have had a better appreciation of this relation than zoölogists. Woodworth (**'94**) has fully realized in a detailed way the influence of the baseleveling processes upon faunal changes.

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[1] I am under obligations to Messrs. Salisbury, Hayes, and Campbell for permission to use their figures and to Prof. E. A. Birge of the Wisconsin Geol. and Natural History Survey for the loan of the cuts for Figs. 1, 2, and 3.

His paper is of great value to the general student as well as to the special student of faunal problems.[1] I find that he had anticipated many of the conclusions to which I had come, but, on account of their imperfect recognition, they will be well worth repeating. Geologists have been primarily concerned with the submarine aspect of physiographic changes. Chamberlin has discussed this in a very suggestive paper ('98).

Since there is a very evident correlation between the erosion of the land and the deposition of the eroded material in the sea, we are able to see that under some circumstances both the submarine and subaerial factors of physiographic change must be taken into consideration in explaining habitats and the struggle for existence of aquatic organisms. This may be illustrated if we suppose that as a continental shelf becomes reduced in area the crowding of its fauna might force some of its members into fresh water, a habitat with a relatively poor fauna, which consequently is open territory.

It appears that many biologists are unfamiliar with the idea of baseleveling. For this reason the following brief account is given, showing how rivers cut down land and tend to reduce it to a baselevel. If a comparatively level country be elevated out of the sea a few hundred feet, and rains begin to work upon it, the slight inequalities of the surface will cause the waters to collect in the hollows and then run off, carrying detritus and cutting a trench or gully. This trench becomes with succeeding rains deeper, wider, and longer as it cuts its way into the uplands, and thus valleys may be formed. With this growth or increase of the area of valleys there is an increase of lowland and cliff habitat and a decrease in the upland habitat. These progressive changes are beautifully shown in Figs. 1, 2, and 3, after Salisbury. It is important to notice here the changes in the relative proportions of the habitats, with a premium placed upon those forms which can occupy the habitat that is increasing in area. These changes will produce tension lines between the inhabitants of the various habitats.

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[1] Dr. H. C. Cowler has recently applied these principles to the study of plants:

The Physiographic Ecology of Chicago and Vicinity; A Study of the Origin, Development, and Classification of Plant Societies, *Bot. Gazette*, vol. xxxi (1901), pp. 73–108, 145–182.

The Plant Societies of Chicago and Vicinity, *Bull. of the Geographic Society of Chicago*, No. 2, 1901.

With regard to the river fauna, at first when the fall of the river is great, rapid-water forms have the advantage, but with the development of sluggish, meandering streams upon bottom land, quiet-water forms find a home. Since the lowland or swampy conditions begin at the mouth of the stream, quiet-water forms will be introduced there, and with the extension up stream of lowland conditions this fauna is led in that direction; similarly, the head of the valley leads *its* rapid-water fauna in the same direction. Thus there is a definite succession of forms working up the valley, and, in a certain sense, by passing down stream one gets a recapitulation of the types of fauna which inhabit a given point of the stream during its ideal history. Dendritic tributary streams help to carry these same conditions in diverging directions, thus leading the fauna in various directions toward the divides.

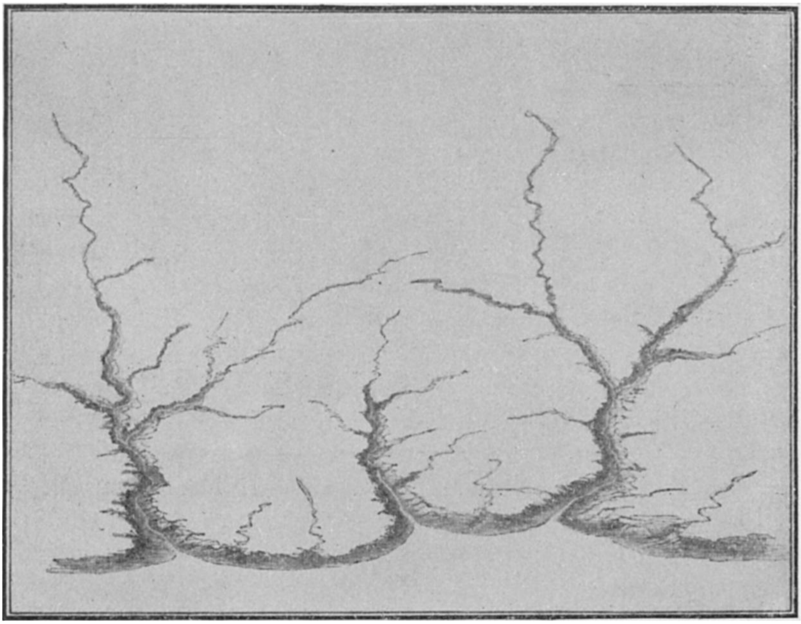

FIG. 1. — Young valleys. (After Salisbury.)

Later on, with the wearing away of the inter-stream uplands, which at first were flat-topped, but which become more and more reduced by the dendritic etchings of the smaller streams, the divides gradually become more sharp, and the country reaches its maximum degree of roughness and cliff habitat, and consequently the greatest isolation of its streams and their faunas. By degrees these sharp divides are lowered, and head-water streams favorably located begin to capture fellow streams with their faunas, and thus there is a mixing of rapid-water faunas.

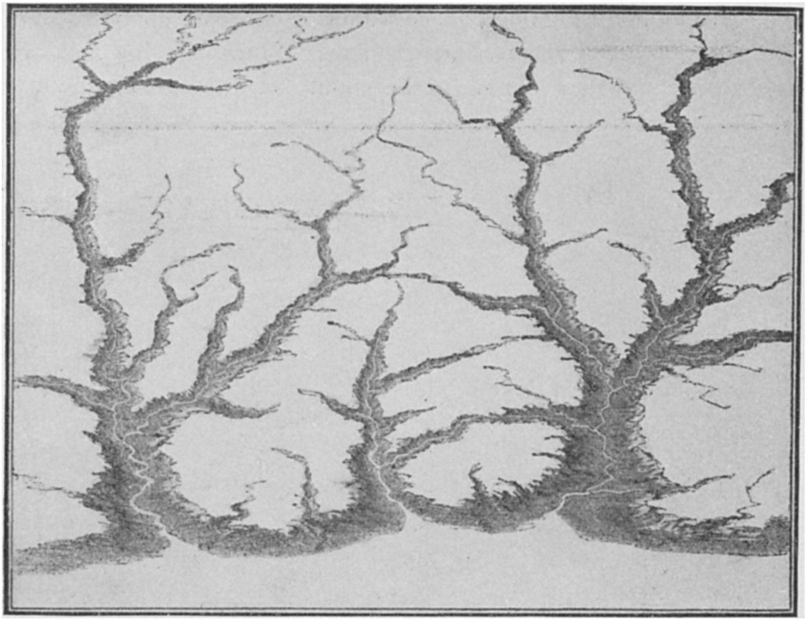

FIG. 2. — Valleys of later stage. (After Salisbury.)

The time of maximum roughness in the topography coincides with that of maximum isolation, but with the fusion and concentration of drainage lines a period begins which favors wide distribution by the removal of barriers; thus in a country approaching baselevel a wide distribution of the fauna will be greatly facilitated with a premium placed upon the lowland fauna. This stage of wide distribution favors interbreeding, and thus a period of swamping by intercrossing may be produced. The cliff fauna would have its maximum distribution and area of habitat when the country was at its maximum roughness.

It will not be necessary here to go further into the details of these processes, as the preceding remarks, with an examination of the diagrams, will suffice to show that these principles may be applied almost indefinitely, but the details vary greatly in different localities. One point perhaps needs special emphasis, and that is, we must think of these processes as *active* and taking place before our eyes.

The bearing of these factors upon the large amount of endemism seen in southeastern United States will be illustrated by a few examples. The physiographic changes of this region have been very carefully studied, but comparatively little has been done to correlate these changes with the geographic distribution of the fauna of this region, and especially with its endemism. I hope, by calling attention to a few of these

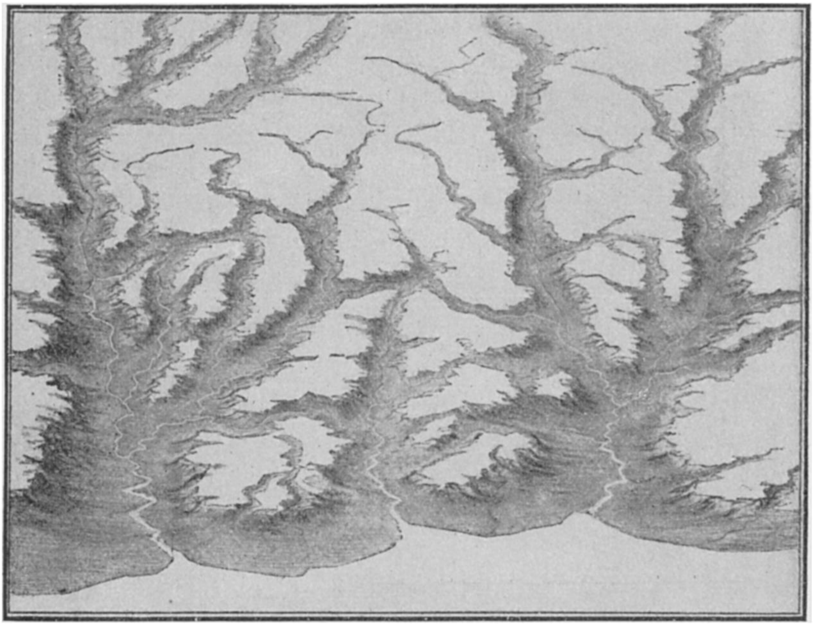

Fig. 3. — Valleys of further development than shown in Fig. 2. (After Salisbury.)

correlations and to some of the principles involved, that others, more familiar with special groups of animals, may be led to make similar comparisons and correlations, and also to emphasize the fact that causal and genetic faunal studies must in the future take into account these factors, if work of permanent value is to be done. Biological surveys will, carried out in this way, become decidedly more than faunal lists, with miscellaneous biological information. In order to emphasize certain aspects of the baseleveling processes special phases will be discussed under separate heads.

Migration of Divides.

The migration of divides has long been recognized as an important factor in the mixing of river faunas, but without a distinct recognition of it as a phase of the baseleveling process. The following examples will show the influence of the migration of divides upon faunas. But first, attention will be called to some of the facts of the distribution of the family Pleuroceridæ, or Strepomatidæ of the older authors. This family is distinctly North American, living forms occurring here only. Tryon's monograph (**'73**) on this family, from which I take my data, recognizes four hundred and sixty-four species. Excepting those species whose exact locality is not definitely known and certain Pacific coast forms, most of these are limited to the Tennessee River and its tributaries above Florence, Alabama, and to the Coosa River. Two-thirds, or about three hundred, of these species are confined to these two river systems.

The region in which this family reaches its maximum development in both individuals and species is remarkably limited and is bounded by Tryon as follows. On the "*North*, by the Tennessee River and tributaries. The Cumberland Mountains prevent the dispersion of the species of this river to the northward until its course is directed into Alabama. Here the character of its species (which we will again allude to further on) changes, and they become gradually less numerous and of greater geographical dispersion as the river runs toward the west. *East*, the mountain range of the Blue Ridge, running southwestwardly into the interior of northern Georgia; thence, the Chattahoochee River and tributaries, to within a hundred miles of the Gulf. *South,* the species are restrained from spreading by the influence of the Gulf of Mexico. *West,* the Alabama, Cahawba, and Black Warrior Rivers and their tributaries, those of the latter reaching almost to Florence, on the

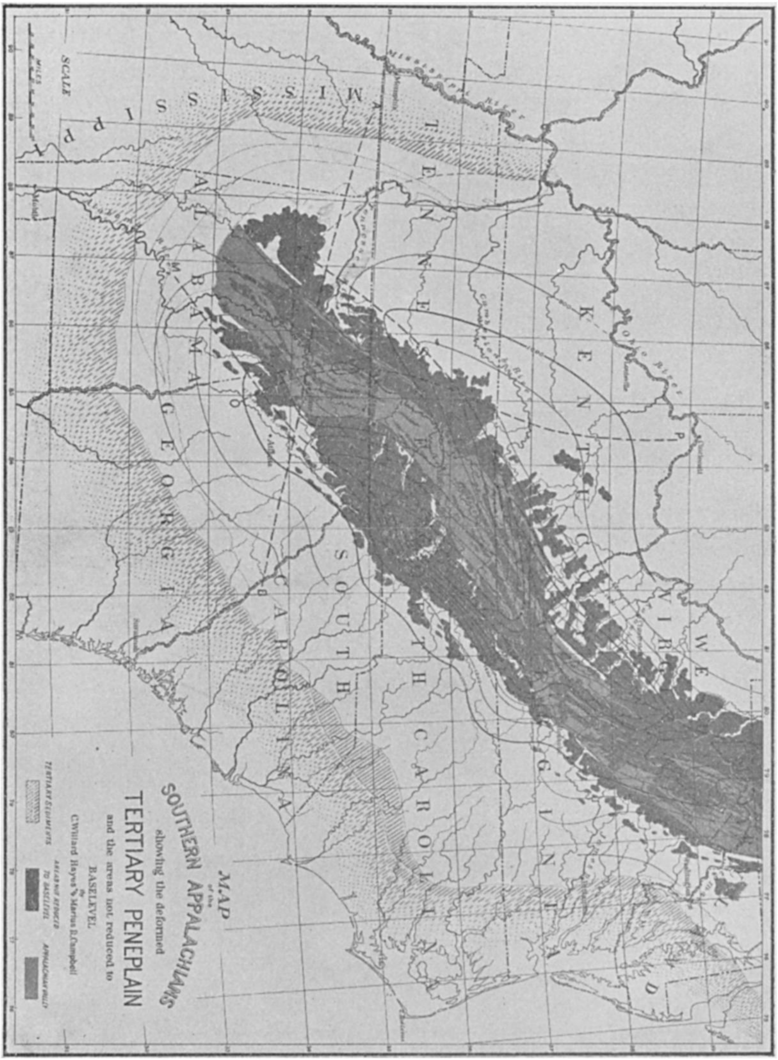

Fig. 4. — Map of Appalachian valley, which is the area of maximum differentiation of the Pleuroceridæ. (After Hayes and Campbell.)

Tennessee River, which may represent the northwestern point of our boundary.

"These limits are necessarily imperfect, but, nevertheless, include at least three-fourths of our species within an area of three hundred miles extent, either north and south or east and west." By reference to Fig. 4 (after Hayes and Campbell), one will see that these limits are practically those of the Appalachian valley, and thus enclose a natural physiographic region.

Again, Tryon remarks: "Assuming the Ohio River as a dividing line, we find that ninety-five per cent of all the species originate south of it."

So much for these general facts of the distribution of this family which are necessary for an understanding of the influence of the migration of the divides upon them.

With the above facts of the distribution of these shells fresh in mind, about two years ago I learned from Hayes's ('95) paper of the view that the upper Tennessee River formerly flowed by way of the Coosa-Alabama Rivers into the Gulf. I saw at once in this an adequate explanation for the peculiar distribution of many of these shells in these two river systems. Since the data for this paper have been collected Mr. C. T. Simpson ('00) has published similar conclusions, drawn from the Unionidæ. According to Hayes's and Campbell's ('94), and also Hayes's ('99), opinion, the Tennessee River above Chattanooga was captured by a westward-flowing stream, and thus led away from the Gulf by the Coosa-Alabama to the Gulf again by way of the Ohio and Mississippi. Thus we see that the region in which the maximum development of this family is reached was *broken into two parts* (Fig. 5). The bearing of this upon the shell fauna is very marked.

This family is divided into two sections, and as to their distribution Tryon (*loc. cit.*, p. xl) says: "While the *Trypanostomoid* forms attain their maximum development in size and number in the Tennessee River, they are to a very great extent replaced by the *Goniobasic* forms in the Coosa River, which is undoubtedly the metropolis of the latter. The most striking genus of each of these groups is absolutely confined to the respective streams in which the groups had their origin.

Thus, Io and Schizostoma are inhabitants, the first of the Tennessee and branches, the second of the Coosa, and neither of them are elsewhere found." This is an excellent illustration of how the migration of a divide may favor differentiation.

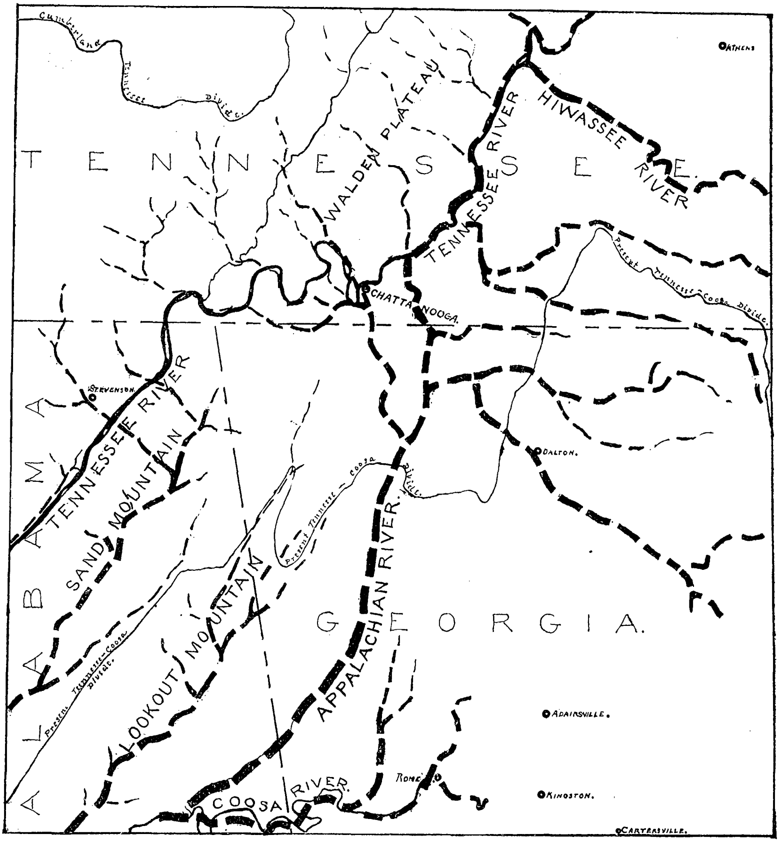

Fig. 5. — Map showing ancient (broken line) and present (continuous line) drainage in the vicinity of Chattanooga. (Adapted from Hayes, '99.)

The family has thus been broken up into two parts, both geographically and biologically.

The genus Pleurocera is credited with eighty-four species, twenty-three of which are found in Tennessee, and twenty-one are apparently peculiar to it. This same genus is represented in the Alabama system by fourteen species, and three of them are peculiar to it. "These species," says Tryon, "are generally confined, however, to those portions of the Coosa and branches that approach to east Tennessee." Lithasia and Pleurocera are other genera divided in their distribution between the two systems. In the genus Strephobasis one species (Bitæniata) is found in the Black Warrior of Alabama drainage and in the Tennessee River at Chattanooga.

In the Goniobasic section there are two types of shells: one group is characteristic of the Tennessee and the other of the Coosa. In the genus Goniobasis, about ten of the elevated smooth species are found in the Tennessee, and about the same number in the Alabama system. Tryon (*loc. cit.*, p. xlviii) says of this genus: "There are over sixty species in the group which I have designated as 'compact and ponderous' for want of a better name. They are essentially a distinct group from the other Goniobases, and all the species except three are peculiar to the branches of the Alabama River."

Consequently, we see that this family reaches its maximum development in two distinct river systems, the upper Tennessee and the Coosa-Alabama, which formerly formed one river system (Fig. 5), and that by the diversion westward of the upper Tennessee, by the migration of its divide, this fauna has been split into two parts, each part having several genera, as well as species, in common. This process has led to an isolation of the Coosa-Alabama fauna and a mixing of the waters of the upper Tennessee with those of the Mississippi valley. In faunal studies some of the most striking peculiarities of the Tennessee River are very apt to be overlooked if we consider it a part of the Mississippi system only.

That these two systems have been separated for a considerable period of time, or that these forms have evolved very rapidly, is shown by the fact that it is the genera or groups of species which are found common to both streams rather than the individual species.

The family Pleuroceridæ is not the only group which has divided by the diversion of the waters of the Tennessee. The family Viviparidæ has a geographical distribution very similar to that of the Pleuroceridæ, its greatest variety being found in southeastern United States. The genus Tulotoma is confined to the upper part of the Coosa River, and Lioplax has two species, one from the Coosa and the other from the Mississippi valley drainage. The species *Campeloma ponderosa* is found in both river systems.

An interesting illustration comes from crayfish. *Cambarus spinosus, extraneous,* and *erichsonianus* are found in both the Tennessee River and in the head-water parts of the Coosa-Alabama system.

A head-water fauna is very different from a lowland fauna; thus a knowledge of the habitats of animals will furnish criteria by which we are able to recognize, to some degree, the conditions under which divides have migrated. Since valleys continually lead their rapid-water fauna to the divides, these forms are the first which become transferred when they are shifted. What evidence is there to support this view? This is well shown if we consider those forms which are the *first* to surmount mountain barriers.

The Rocky Mountains have been a very formidable barrier to our fauna, there being but few passes or gaps through them. The fish fauna on each side of these mountains in the United States are remarkably distinct, but two species, according to Jordan ('96, p. 118), are found on both sides of this great barrier, and these species are very naturally rapid-water species, and not lowland forms. These two fish are the Rocky Mountain trout (*Salmo mykiss* Walb.) and the Rocky Mountain whitefish (*Coregonus williamsoni* Gir.). In the Appalachian Mountains the upland living brook trout (*Salvelinus fontinalis* Mitch.) illustrates the same point, it being found on both sides of the range.

Extension of Lowland Faunas into Uplands by Baseleveling.

River valleys are well known as highways for the dispersal of animals. These valleys, of course, are not always due to the process of baseleveling, but in the southeastern Appalachians we have good illustrations of the extension of a valley due to this process. The valley of the Tennessee River above Chattanooga is an excellent illustration of this. By means of a narrow neck of lowland being carried back into the uplands an isolated, elongated land habitat is developed which reminds one of river isolation. Merriam's Life Zone Map ('98, plate) shows that there is an extension of the Upper Austral Zone into the Transition Zone due to the Tennessee valley. With the baseleveling process the isotherms gradually migrate up the valley and thus help to make it possible for the fauna to follow. Of course valleys, of whatever origin, may act as highways of dispersal.

It is important in this connection to recall the more or less definite succession of forms up the valley, because the problem of dispersal among some animals is largely a problem of the *continuous* distribution of the habitat.

Segregation of the Upland Faunas by Valleys.

Correlated with the extension of the valleys into uplands is the segregation of the uplands by the growth of the valley. This influence is beautifully shown by the land shell fauna on each side of the Tennessee valley. Since the Tennessee valley divides the uplands of the Cumberland plateau from those of the Smoky Mountains, I was led to anticipate that this isolation, which has existed for a considerable period of time, would show upon the land shell fauna, because these animals are very sensitive indicators of such influences. Later I was interested to learn that Pilsbry ('00) had very recently divided the "Cumberland sub-region" of Binney into an eastern and western division, corresponding to the uplands segregated by the Tennessee valley. He gives about twenty species and varieties characteristic of the Cumberland plateau, and about twenty-five to the Smoky Mountains. The French Broad River has for a long time separated the Great Smokies from Roan Mountain, and corresponding with these facts it has been found that six forms are peculiar to Roan Mountain and about a dozen to the Smoky Mountains.

Influence of Baseleveling upon Tension Lines.

The relation of the faunas of the different levels or baselevels to each other is also important from the standpoint of tension zones. On account of the large area which they may occupy at certain stages of topographic development these zones have great importance, for in them there is a large population subject to a peculiar environment and hence liable to important evolutionary changes. A stage of equilibrium is not reached here, as erosion makes this area relatively unstable and subject to continual changes. It is important to determine which is the more powerful, the physiographic or organic influences, in the production of these lines. The powerful influence of the physiographic processes in general leads one to expect that at first the physiographic factors will dominate, but later, in a fairly uniform habitat, the struggle will become more organic. In the study of dispersal and distribution of animals, it is important to see that the physical conditions lead, and that in a more or less definite succession the flora and fauna follow; thus the fauna comes to fit the habitat as a flexible material does a mold.

The time is passed when faunal lists should be the aim of faunal studies. The study must not only be comparative, but *genetic*, and much stress must be laid on the study of the habitat, not in a static, rigid sense, but as a fluctuating or periodical medium. The bearing of faunal studies upon the problem of differentiation and the origin of species, is very close, and in our search for the factors we must not lose the perspective, and overlook those factors which are fundamental and work through long periods of time.

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REFERENCES.

'98 CHAMBERLIN, T. C. A Systematic Source of Evolution of Provincial Faunas. *Journ. of Geol.* Vol. vi, pp. 597–608.

'95 HAYES, C. W. The Southern Appalachians. *Nat. Geograph. Monogr.* Vol. i, No. 10.

'99 HAYES, C. W. Physiography of the Chattanooga District in Tennessee, Georgia, and Alabama. *Nineteenth Ann. Rep. U. S. Geol. Survey*, 1897–98. Pt. ii, pp. 1–58, Pls. I–V.

'94 HAYES, C. W., and CAMPBELL, M. R. Geomorphology of the Southern Appalachians. *Nat. Geograph. Mag.* Vol. vi, pp. 63–126, Pls. IV–VI.

'96 JORDAN, D. S. Science Sketches. New edition. Chicago.

'98 MERRIAM, C. H. Life Zones and Crop Zones of the United States. *Bull. No. 10, Division of Biol. Survey, U. S. Dept. of Agriculture.*

'00 PILSBRY, H. A. Mollusca of the Great Smoky Mountains. *Proc. Acad. Nat. Sci. of Philadelphia* (1900), pp. 110–150.

'00 SIMPSON, C. T. On the evidence of the Unionidæ regarding the Former Courses of the Tennessee and the Other Southern Rivers. *Science.* Vol. xii, N.S., pp. 133–136.

'73 TRYON, G. W. Land and Fresh-Water Shells of North America. Pt. iv, Strepomatidæ. *Smithsonian Miscellaneous Collections, No. 253.* Washington.

'94 WOODWORTH, J. B. The Relation between Baseleveling and Organic Evolution. *Amer. Geologist.* Vol. xiv, pp. 209–235.

REFERENCES ON THE BASELEVELING PROCESSES.

'77 GILBERT, G. K. Report on the Geology of the Henry Mountains. *U. S. Geog. and Geol. Survey, Rocky Mountain Region.* Chapter V. Land Sculpture.

'00 SALISBURY, R. D., and ATWOOD, W. W. The Geography of the Region about Devil's Lake and the Dalles of the Wisconsin, with Some Notes on its Surface Geology. *Wis. Geol. and Nat. Hist. Survey, Bull. No. V.* Educational Series, No. 1. Chapter III. General Outline of Rain and River Erosion.